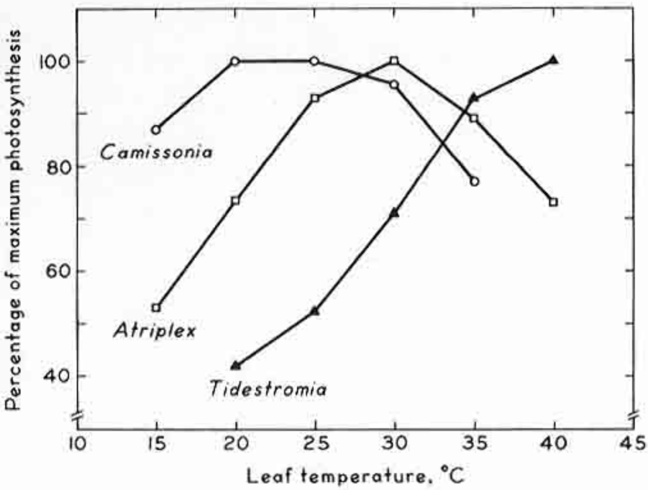

Fig. 25. Seasonal photosynthetic temperature responses of three plant species native to the floor of Death Valley. Measurement conditions as given in Fig. 24.

chemical energy with an efficiency of 8.5%. This is a consequence of the lack of light saturation at midday irradiances, a feature that is also characteristic of *Tidestromia* (*Year Book 70*, pp. 540–550). The *in situ* midday photosynthetic rate of *Camissonia* was nearly 6 nmol CO_2 $cm^{-2}sec^{-1}$, a rate that is higher than has been measured on such productive crop species as corn, sorghum, and sugar cane.

The thermal optimum of photosynthesis of the various species coincides with the prevailing temperatures during their principal growing period (Fig. 25). The winter-active C_3 *Camissonia* has a thermal optimum near 20°C and the summer-active C_4 *Tidestromia*, of over 45°C. The C_3 plant *Larrea* can potentially grow throughout the year, except during midsummer. This plant shifts its thermal optimum in concert with the prevailing air temperatures. The C_4 plant *Atriplex* grows only during the winter and spring months and maintains a thermal optimum at 30°C.

The major results from these studies will be published elsewhere in greater detail along with a full analysis of the physiological components responsible for the changing seasonal photosynthetic responses of the plants.

This work was supported in part by the National Science Foundation. We thank the U.S. Park Service in Death Valley for their considerate assistance.

LEAF ABSORPTANCE AND PHOTOSYNTHESIS AS AFFECTED BY PUBESCENCE IN THE GENUS *Encelia*

James Ehleringer

Among higher plants there is a trend toward increasing leaf pubesence (presence of leaf hairs) along environmental gradients of decreasing precipitation (Schimper, 1903; Warming, 1909; Clausen, Keck, and Hiesey, 1940). These hairs, covering the surface of the leaf, are generally considered to be an adaptive feature of plants occupying arid habitats. The reason is that pubescence can reduce the heat load of leaves by increasing the reflectance from the leaf surface, reducing the amount of radiation absorbed. The adaptive value of a reduced heat load to plants growing in hot or arid climates is great because it can result in lower leaf temperatures and less transpirational losses.

In the southwestern United States and northern Mexico there are several species of the genus *Encelia* (Compositae), each species characteristically showing differences in its degree of pubescence and each occupying habitats differing in precipitation and temperature. Two extremes of leaf pubescence in *Encelia* are *E. farinosa*, a drought-deciduous shrub with white, densely pubescent leaves, and *E. californica*, also drought-deciduous, but with green nonpubescent leaves (Fig. 26). The two species are allopatric in their distributions: *E. californica* is restricted to the relatively moist coastal regions of southern California and northern Baja California, and *E. farinosa* occurs in the dry desert areas of the southwestern United States and northern Mexico.

The absorption spectra of leaves from each of these two species were measured between 400 and 700 nm (visible light) to determine to what extent pubescence was modifying light absorption. The waveband between 400 and 700 nm was chosen because (1) it is these wavelengths that are useful for the photosynthetic process, and (2) some 80% of the sun's light that is normally absorbed by green nonpubescent leaves is in this waveband. Light absorptance of intact, metabolically active leaves was measured monochromatically using an Ulbricht sphere (Rabideau *et al.*, 1946). Solar absorption coefficients for the 400–700 nm spectral range were calculated from

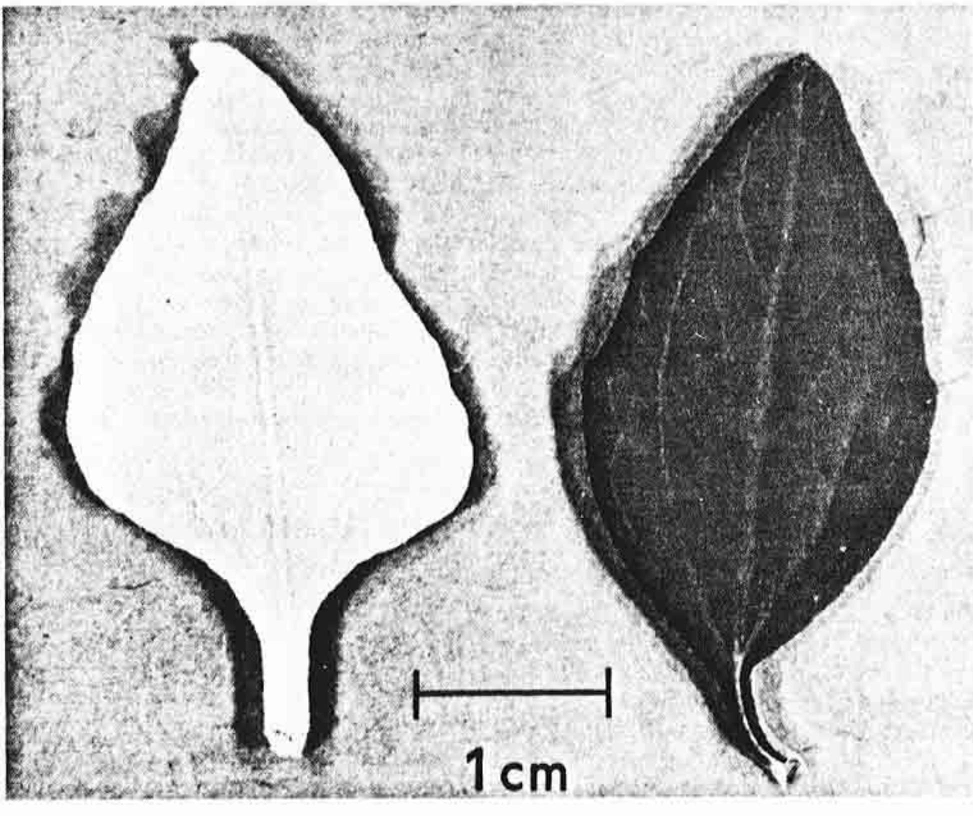

Fig. 26. Typical leaves of the white pubescent *Encelia farinosa* (left) and green nonpubescent *E. californica* (right).

the absorption spectra of the upper leaf surface in conjunction with the solar spectrum at the earth's surface. The solar absorption coefficients represent the integrated percentage of quanta absorbed by the leaf over the photosynthetically active wavelengths. The percentage of quanta absorbed is not necessarily equivalent to the percentage of energy absorbed, since quanta of different wavelengths contain different amounts of energy. Over the range 400–700 nm, however, the percentages were nearly identical for leaves of *Encelia*.

Absorption spectra for a nonpubescent *E. californica* and a very pubescent *E. farinosa* were measured and have been published elsewhere (Ehleringer *et al.*, 1976). The nonpubescent *E. californica* exhibited a spectrum typical of intact green leaves (*Year Book 64*, pp. 420–425; Gates *et al.*, 1965), but in the pubescent *E. farinosa*, the absorptance values were sharply reduced (Ehleringer *et al.*, 1976). The transmittance through the leaf hairs was less than 1%. This low transmittance and high reflectance at all wavelengths indicated that the pubescent layer was serving as a blanket reflector, decreasing the light absorbed by approximately 56% below the values of *E. californica* at all wavelengths. The differences between the two spectra were due only to differences in pubescence. The chlorophyll contents of leaves from both species were equivalent (about 40 μg cm^{-2}), and the thickness of the epidermis and that of the mesophyll layers were similar. Solar absorption coefficients for the examples described were 84.8% and for *E. californica* and 29.0% for *E. farinosa*. The degree of pubescence appears most certainly to modify energy absorption by the leaf. In the example described the pubescent *E. farinosa* is absorbing only 29% of the incident radiation between 400 and 700 nm. This value represents only 34% of the radiation being absorbed by the nonpubescent *E. californica* leaf over the same waveband.

If this pubescence layer is indeed acting as a blanket reflector, removal of the pubescence from *E. farinosa* should yield a spectrum similar to that of *E. californica*. Figure 27 shows the absorption spectra for a leaf of *E. farinosa* with hairs intact, the same leaf after the pubescence has been removed, and, for comparison purposes, the absorption spectra of an intact *E. californica* leaf. As shown, once the pubescence of *E. farinosa* has been removed, it is not possible to distinguish the spectrum of that leaf from the spectrum of nonpubescent *E. californica*. This comparison provides conclusive evidence that between 400 and 700 nm the pubescence layer is serving as a blanket reflector and that it is not preferentially reflecting particular wavelengths.

In addition to variation in pubescence between species there are temporal or seasonal changes in absorptance among some of the pubescent species. To illustrate this, the seasonal course of solar absorption coefficients was measured in leaves of the pubescent *E. farinosa* and nonpubescent *E.*

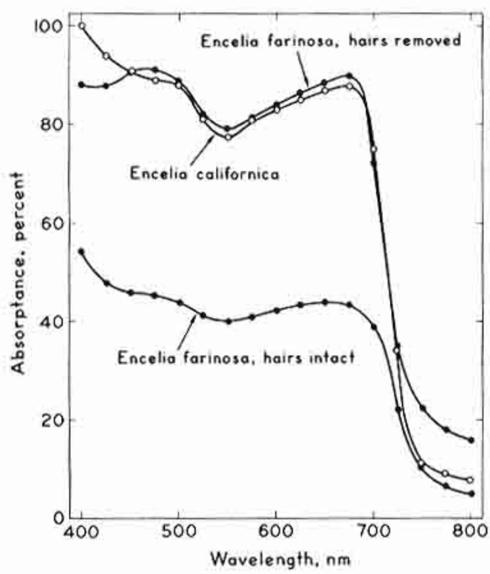

Fig. 27. Absorption spectra from 400 to 800 nm of intact leaves of *Encelia farinosa* with hairs intact and after hairs had been removed, compared to the spectrum of *E. californica*.

californica. Field observations of solar absorption coefficients for both species were made in December (1974), March (1975), and July (1975). *E. californica* was sampled at Point Mugu (362 mm mean annual precipitation) and San Diego (240 mm) in southern California. *Encelia farinosa* was sampled at Superior (433 mm), Tucson (270 mm), Tonopah (155 mm), and Ehrenberg (90 mm) in southwestern Arizona. Five representative samples were collected from each site. The means of all samples of a species at a given sampling time were reduced to a single value.

As shown in Fig. 28 the mean solar absorption coefficients for *E. californica* were 83.9%, 83.8%, and 82.4% and for *E. farinosa* 71.7%, 63.4%, and 52.5%, respectively, for sampling dates of December, March, and July. The range of values between sites averaged 2% for *E. californica* and 10% for *E. farinosa*, while the range within a site averaged 2% for both species. These field data clearly show that the solar absorption coefficient for *E. californica* remains higher than that for *E. farinosa* at all times through the growing season. Additionally, whereas the solar absorption coefficients for *E. californica* remained constant through the season, the absorption coefficients for *E. farinosa* steadily declined as the season progressed. By July *E. farinosa* averaged 30% less visible light absorbed than *E. californica*. This decrease in leaf absorptance by *E. farinosa* through the season occurred in conjunction with an increase in mean maximum air temperatures. This correlation suggests a role for pubescence in modifying the leaf energy balance as the environment becomes harsher and reduces leaf temperatures. Cunningham and Strain (1969) have also shown that leaf size decreased through the season, further providing a more favorable energy balance.

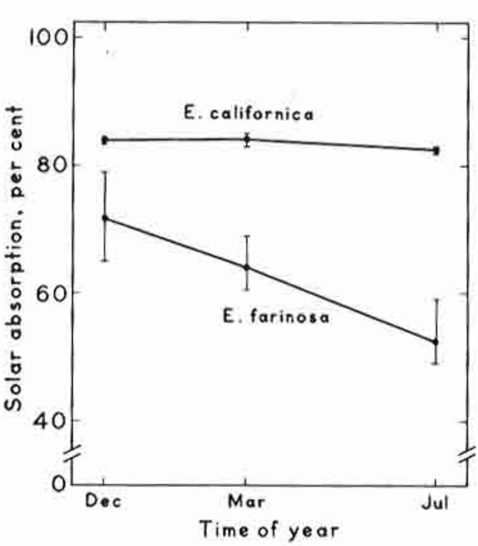

Fig. 28. Seasonal course of changes in the solar absorption coefficients in leaves of *Encelia californica* and *E. farinosa*. Points represent means of samples from different sites, and vertical bars represent the ranges of values between sites.

If pubescence is adaptive for *E. farinosa*, then a positive correlation should exist between leaf absorptance and precipitation for sites occupied by this species. Solar absorption coefficients from each of the *E. farinosa* during March, the period of peak productivity, were plotted against the precipitation received up to the sampling date at the site during the current growing season (Fig. 29). These data reveal a strong correlation ($r^2 = 0.995, P < 0.01$) between the solar absorption coefficient and precipitation, suggesting, first, that the reduction in energy absorbed by pubescent leaves is directly dependent on the aridity of the environment and, second, that the degree of pubescence is a plastic response by the leaves to the amount of precipitation received. Since transmittance through pubescent leaves is quite small, there is also a strong correlation between the solar reflection coefficient and precipitation. It should be noted that it is the plastic response by pubescent leaves which is responsible for most of the variation in solar absorption coefficients between *E. farinosa* sample sites. The possible correlation between pubescence and aridity on a community basis rather than on a single

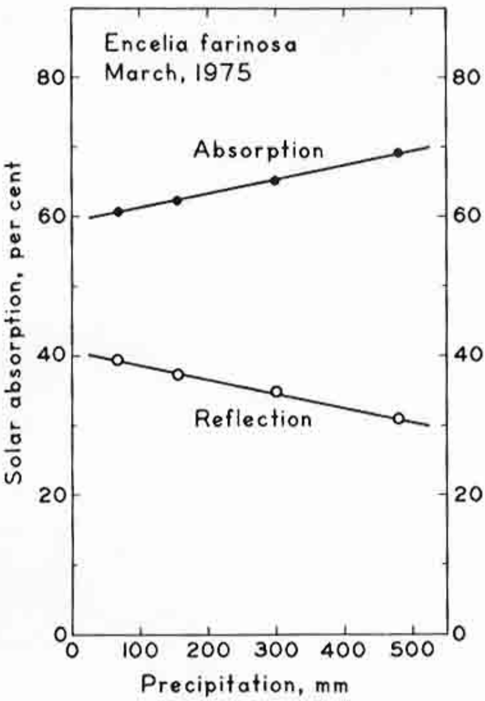

Fig. 29. Solar absorption coefficients for leaves of *Encelia farinosa* on several sites plotted as a function of the seasonal precipitation received at that site during current growing season.

species basis was discussed by Billings and Morris (1951), but solar absorption coefficients were not reported.

The decrease in light absorbed by pubescent *E. farinosa* leaves over the 400–700 nm waveband is sufficient to cause significant reduction in the heat load of leaves. This decreased radiation load should indeed be of selective advantage to *E. farinosa* in arid desert sites since nearly 50% of the solar radiation load on the leaf and approximately 80% of the radiation absorbed by typical green leaves is in the 400–700 nm range. Yet a reduction in the amount of light absorbed carries with it a great disadvantage because reduction in light absorption means less light is available for photosynthesis. To minimize these effects of pubescence on light-limited photosynthesis it is likely that there is an inverse relationship between the degree of pubescence and the water available to the plant, such that as plants are less stressed the degree of pubescence is lowered. The strong correlation between solar absorption coefficients and precipitation (Fig. 29) serves as indirect evidence for such a relationship.

To determine to what degree the advantages of pubescence—in terms of reduced heat load on the leaf—may be offset by lower rates of carbon gain, photosynthetic rates were measured on individuals of *E. farinosa* differing in degree of pubescence. All plants were grown under conditions of sufficient water and nutrients and full sunlight in phytocells (*Year Book 72*, pp. 393–403). Simultaneous measurements of CO_2 and water vapor exchange were made on single attached leaves using a leaf chamber and gas-exchange system (Mooney *et al.*, 1971; Osmond and Björkman, 1975). All measurements were made in normal air, 325 μbars CO_2, and 21% O_2.

Photosynthesis-light response curves for leaves of *E. farinosa* with solar absorption coefficients of 53%, 65%, and 82% are shown in Fig. 30. Three significant features evident in these curves are: (1) The incident quantum yield (slope of linear part of curve between 0 and 30 nE cm^{-2} sec^{-1}) decreases as the pubescence increases; (2) the maximum rates decrease as pubescence increases; and (3) unlike most plants, net photosynthesis under all three pubescence conditions is not light saturated even at 200 nE cm^{-2} sec^{-1}, which is equivalent to full noon sunlight during the summer. Quantum yields on an incident light basis were 0.025, 0.033, and 0.041 for absorptances of 53%, 65%, and 82%, respectively. When calculated on an absorbed quanta basis, the quantum yields were 0.048, 0.050, and 0.050. These quantum yields, typical for higher plants (*Year Book 74*, pp. 760–761), indicate that although pubescence in *E. farinosa* increases light reflectance and reduces net photosynthesis, it does not affect the basic photosynthetic process (CO_2 fixed per

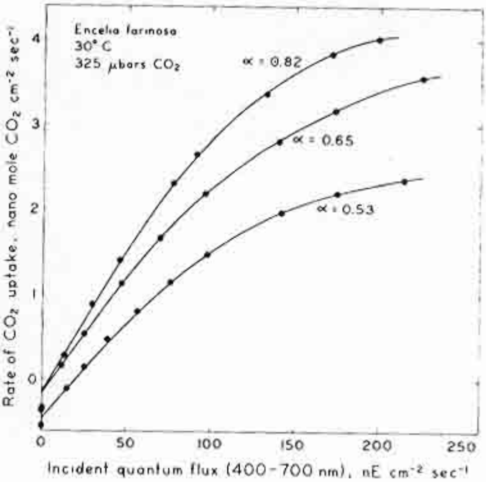

Fig. 30. Light dependence of net CO_2 uptake by single attached leaves of *Encelia farinosa* differing in their degree of pubescence. Rates were determined at a leaf temperature of 30°C, a CO_2 partial pressure of 325 μbar, an O_2 concentration of 21% by volume, and a water vapor pressure deficit of less than 10 μbar. α = absorption coefficient.

quantum absorbed). Net photosynthesis is so dramatically affected by pubescence that at a leaf absorptance of 53% the net photosynthetic rate is nearly linear with light intensity up to full sunlight. Stomatal conductances to water and CO_2 exchange were similar for the leaves at any given light intensity, suggesting that CO_2 diffusion limitations were not responsible for differences among the curves. When photosynthetic data from these three curves are plotted against absorbed rather than incident quanta, all data lie on a single curve, indicating that the principal differences among the curves were due primarily to decreases in light absorption due to pubescence and not to physiological differences.

Studies on the ecophysiology of the genus *Encelia* will continue in the oncoming year. Having documented the extraordinary capability of the pubescence layer to reflect light and also to affect physiological processes, this coming year's work will focus on three main questions that have arisen during the past year: (1) What are the causes of the extremely high photosynthetic rates observed in leaves of *Encelia* species? (2) What other heat transfer or energy balance functions does the pubescence layer have? In particular, does the pubescence serve as an insulating layer between the metabolically active tissues and the hot, arid external environment? (3) What are the ecological relationships in the tradeoff between carbon gain and reduced heat load on the leaf in pubescent leaves along aridity gradients?

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CARBON DIOXIDE AND TEMPERATURE DEPENDENCE OF THE QUANTUM YIELD FOR CO_2 UPTAKE IN C_3 AND C_4 PLANTS

James Ehleringer and Olle Björkman

Last year we reported that at a leaf temperature of about 30°C and in normal air the quantum yield for CO_2 uptake in plants possessing the C_3 path-